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DEVELOPMENT OF THE BRACHIAL SUPPORTS IN DIELASMA AND ZYGOSPIRA.

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It has been shown by several authors* that the brachial supports in the Terebratellidæ pass through a series of distinct metamorphoses during the life of the animal. In the higher genera, these stages may be correlated with the adult structures of lower forms, thus furnishing satisfactory data for a systematic arrangement of the genera and for their phylogenetic relations.

This kind of research naturally requires ontogenetic series of considerable completeness, and it is often difficult or impossible to obtain such material representing fossil forms. Moreover, the fossils must be exceptionally well preserved to afford a means of working out the development of a structure so delicate as the calcareous lamellæ supporting the brachia, especially in young specimens from one to five millimeters in length.

It first seemed desirable to determine the development in some genus of the Terebratulidæ from the Paleozoic, in order to ascertain whether the brachial supports as in Neozoic and recent forms passed through a series of transformations, and to determine the most primitive form of the loop in the Ancylobrachia. For this purpose, a species of *Dielasma* (*D. turgida*) obtained from Mr. Moritz Fischer was used. The specimens are

* Davidson, Friele, Deslongchamps, Fischer and Œhlert, and Beecher.

from the St. Louis group of the Lower Carboniferous in Kentucky. The shells are partially silicified, generally filled with transparent calcite, and afford very satisfactory preparations of the arm supports. It was found that the loop of *Dielasma* underwent transformations during growth, and that the earliest stage observed is like *Centronella*. This establishes the *centronelliform* loop as the simplest type of loop in the Ancylobrachia. Besides *Centronella*, other adult representatives of the same structure are *Rensselæria* and *Newberria*. They are all late Silurian, Devonian, and Carboniferous genera, but the *centronelliform* structure continues later, and is represented in the Trias by the genera *Juvavella* Bittner and *Nucleatula* (Zugmayer) Bittner.

It was at once suggested that interesting results would be obtained in studying the development of a spire-bearing brachiopod, and, as the earliest species more clearly show their phylogeny in their ontogeny, the ancient genus *Zygospira* was selected. Very complete material was accessible, collected by the writers from the Trenton of Minnesota and Kentucky, so that series of specimens were assembled representing all stages of growth from specimens .8 mm. in length to mature size. They were prepared to show their brachial supports, and it is clearly demonstrated that the primitive arm support in *Zygospira* is a terebratuloid loop having a *Centronella*-like form, which undergoes several modifications before the growth of the spiral lamellæ, and thus in so far resembling the development of *Dielasma*.

These results threw doubt on a number of Lower and Upper Silurian species described as having recurved loops and previously referred to the higher terebratuloid genera *Macandrevia* or *Waldheimia*. The shells are impunctate, while *Rensselæria* and *Centronella* are distinctly punctate, like all other well-known terebratulæ. Upon investigation, it has been ascertained by Hall and Clarke and the authors that the species which have been referred to *Hallina* and *Macandrevia* from the Silurian are spire-bearing forms, and therefore do not belong to the Ancylobrachia.

Fischer and Œhlert have called attention to a number of recent species which have been erroneously based upon the immature stages of higher species, and in the Terebratellidæ it is evident that great uncertainty must exist in the identification ot specimens not fully adult. Now, finding that Paleozoic genera of both loop and spire-bearing stocks (Ancylobrachia and Helicopegmata) in the adolescent period likewise pass through metamorphoses representing the structures of other genera and even other suborders, it is manifest that species cannot be referred to their proper genera nor genera correctly defined unless the individuals studied are adult and their characters constant for a definite period of time.

Development of the Loop in Dielasma turgida.

The earliest stage thus far observed was found in a specimen a little over four millimeters in length (plate x, fig. 1). The loop at this time is composed of two broad descending lamellæ, which begin at the ends of the crura and extend forward, curving ventrally until they unite in the median line, forming an angular ridge, acuminate in front. As previously mentioned, this structure is very similar to that of *Centronella*, and this stage is therefore called the *centronelliform* stage.

The first change in the form of the loop is brought about by a resorption of the pointed anterior portion, so that the outline is reëntrant in front (fig. 2). Further resorption in the same manner results in the production of two posteriorly directed branches, as shown in fig. 3. This form may be considered as an early immature *Dielasma* loop, as subsequent growth does not materially modify its general characters.

The adult loop, represented in figs. 4–6, differs from the early *Dielasma* stage chiefly in the divergence of the descending branches.

In the *centronelliform* stage the lamellæ converge, and the loop extends half the length of the shell. Both of these relations gradually alter until, in the early *Dielasma* stage, the descending branches are nearly parallel, the loop extends less than half the length, and, finally, when mature, the descending branches diverge and the loop is two-fifths the length of the dorsal valve.

The natural inferences to be drawn from the development of the loop in *Dielasma* are, that *Centronella* represents a larval or immature condition of the higher genera, and that the *centronelloid* loop is the primitive type in the Terebratulidæ. Therefore, as *Centronella* and the closely related genus *Rensselaria* are the only early punctate terebratuloids known, and as they have the primitive type of loop, there arises the question of the validity of the Upper and Lower Silurian species with recurved loops, referred to *Waldheimia* and *Hallina*.

Hall and Clarke (Pal. N. Y., vol. VIII, part ii, pp. 147–153, not yet published) describe and figure the brachial supports in *Hallina*, showing that both *H. nicoletti*, Winchell and Schuchert and *H. saffordi*, W. and S. are provided with short spires of about one volution, connected by a transverse band, as in *Zygospira*. In removing the ventral valve and exposing the loop from that side, as is often done, the short spiral lamellæ have been overlooked. Similar observations have been made by the present writers, so that the systematic position of these forms is now established.

Specimens of *Waldheimia bicarinata* Angelin, from the Upper Silurian of Gotland, were also examined. They were found to possess well-defined spiral cones, and in other respects agreed with the diagnosis of *Dayia*. These facts indicate that the specimens described by Davidson as *Waldheimia mawii* (Fossil Brachiopoda, Supp. vol. IV, part V, pl. iv, figs. 1–3) are the young of *Dayia navicula* Sowerby, sp. (*ibid.*, pl. v, figs. 1–4).

Development of the brachial Supports in Zygospira recurvirostra.

The smallest specimen in which the internal structure was observed measures about 1.33 mm. in length (plate x, figs. 7, 8). The brachial supports consist of two straight, ventrally concave, primary lamellæ, rapidly increasing in width from the thin crural plates to near the center of the valve, where they unite, forming a plate with a central angular ridge. The anterior end of the plate is pointed as in *Centronella*.

In a specimen about 2 mm. in length (figs. 9, 10), the primary lamellæ are practically of the same form as in the preceding, but much of the original central portion of the loop has been resorbed, so that the lamellæ are connected by a short but comparatively wide, ventrally arched, transverse band. The lamellæ, or descending branches, are also more spreading anteriorly, and there is a slight deflection at the crural points, which becomes more and more pronounced as growth progresses.

In the next stage (fig. 11), which has a length of 2.33 mm., the descending branches are more diverging, and the transverse band is longer and more broadly excavated in front.

The succeeding stages here described are based upon material derived from near the top of the Trenton, where the specimens of this species are usually larger and more transverse than those from near the base of the Trenton, which is the horizon of the specimens illustrated in figs. 7–11. Therefore, when the loop in fig. 9 is compared with that of fig. 12, it is seen that the latter is much the wider, from the greater size and breath of the shell, which has at this stage a length of 3.33 mm., while the former is but 2 mm. long. The loop in fig. 12 is somewhat more advanced than in fig. 9, the transverse band being narrower and slightly elevated posteriorly, some resorption having taken place along the inner edges of the primary lamellae. Further resorption in same direction produces the brachial support illustrated in fig. 14. This form of loop in *Z. nicoletti*, *Z. saffordi*, and *Z. recurrirostra* from the lowest Trenton is retained to maturity. However, in specimens of *Z. recurrirostra* from the upper Trenton the posteriorly curved, transverse band is not a mature feature, since it becomes changed into the form represented in fig. 15. In previous stages the transverse band is ventrally arched, but it now bends dorsally, and remains so during subsequent growth until near maturity, when the sinus of the dorsal valve causes it to assume a sigmoid curve.

The spirals next begin to develop (figs. 16 and 17) as two slender converging lamellae, curving toward the ventral valve and originating from the outer pointed ends of the loop. These lamellae then incurve dorsally and laterally to a point just posterior to the transverse band, forming the first volution of a spiral (fig. 18). In this manner further growth and elongation of the lamellae continue until maturity is attained, when there are about three volutions in each spiral cone (fig. 20). The calcareous brachial supports occupy about the same relative space in the shell cavity in all stages of growth.

Observations and Correlations.

Zygospira is the earliest spire-bearing genus known, as it is found in the Birdseye limestone of the Trenton period. It is of considerable interest, therefore, to study the development of the spirals. From the ontogeny, it is shown that the brachial supports in *Zygospira* begin as a loop greatly resembling that of Devonian *Centronella*. Moreover, the loop passes through a series of metamorphoses before the spirals make their appearance.

The most ancient species are *Z. nicoletti* and *Z. saffordi*, small semiplicate forms, in which the spirals are very rudimentary, consisting of about one volution. In the same geological horizon occurs *Z. recurvirostra*, having from two to two and one-half turns of the lamellæ in each spiral. The same species from the upper Trenton has three volutions, while in *Z. modesta* of the middle Lorraine there are from four to five whorls (fig. 25). In *Z. headi* (fig. 24), a large globose finely striated species of the upper Lorraine, there are six whorls to a cone. The geological history, therefore, shows a gradual increase of from one to six turns of the lamellæ in each spiral.

The transverse band connecting the primary lamellæ also undergoes a series of changes. It has been shown that the centronelloid loop (fig. 7) passes into one having the lamellæ joined by a posteriorly directed, transverse band (fig. 14). This form of loop is retained as a mature feature in the brachia of *Z. nicoletti*, *Z. saffordi*, and in the lower Trenton varieties of *Z. recurvirostra*. Passing to the specimens of the latter species, which are geologically later, the band no longer joins the lamellæ as far anteriorly as in the older variety (fig. 20). The point of connection in *Z. modesta* is variable (figs. 25 and 26), but is usually more posterior than in *Z. recurvirostra*, while in *Z. headi* it is manifestly more posterior than in any of the older species of *Zygospira*. The transverse band is now no longer arched backward, but is just the reverse (fig. 24), while its position is progressively more and more posterior, and the loop is gradually shortened before the spirals make their appearance. The gradual increase in the number of the whorls in each spiral and the recession of the transverse band have gone on together.*

The family Atrypidæ includes the genera *Zygospira*, *Glassia*, *Cœlospira*, *Anoplotheca*, *Atrypa*, and *Dayia*. It is easily distinguished from all other families comprised in the suborder Helicopegmata, since the spirals are between the first descending branches of the lamellæ, while in the Spiriferidæ, Nucleospiridæ, and Athyridæ the primary lamellæ are between the spirals.

The gradual increase in the number of whorls in the spirals and the pushing backward of the transverse band in the Atrypidæ is carried farthest in the species of *Atrypa*. In *Cœlospira*

* The extreme anterior position of the transverse band in *Z. recurvirostra* is therefore of no more than specific value, and on this account *Anazyga* Davidson cannot well be separated from *Zygospira*.

barrandei and *C. marginalis* the brachial supports, as worked out by Davidson and Glass, consist of about five volutions, and are similar to those of *Zygospira*, except that the transverse band is more posterior, since it originates near the ends of the crura. This mature condition of *Cœlospira* is seen to be a young condition of *Atrypa* (Davidson), but, as the spirals are more loosely coiled and the transverse band always continuous, this genus should be regarded as valid in the evolution from *Zygospira* to *Atrypa*. In mature *Atrypa reticularis* from the Upper Silurian, there may be as many as sixteen volutions in each spiral cone (Davidson), but more often the number is smaller. The transverse band in this species during its young stages is continuous, but in the adult condition it seems to be usually disunited in the middle. This feature becomes a distinct adult character in the Devonian specimens, which also have a greater number of whorls in the spirals, as shown in a Chemung specimen of this species in Yale University Museum, having twenty-four turns of the lamellæ in each spiral.

The ontogeny and phylogeny of the species of *Zygospira* indicate strongly that the *Atrypidæ* had its origin in a form with a centronelloid loop. A further natural conclusion from the same evidence is that the Ancylobrachia are older and more primitive than the Helicopegmata.

Explanation of Plate X.

Dielasma turgida.

Figure 1.—The *centronelliform* stage of the loop; ventral view. × 6.
2.—A later stage, showing the resorption of the anterior portion of the loop. × 6.
3.—Early *Dielasma* stage, produced by further resorption of the centronelloid loop. × 6.
4.—Loop and crural plates of mature specimen. × 6.
5.—Profile of the connecting band. × 6.
6.—Side view of the loop, crura, and septum. × 6. St. Louis group, *Kentucky*.

Zygospira recurvirostra.

Figure 7.—*Centronelliform* stage of the loop. × 12.
8.—Profile of same. × 12.
9.—A later stage; showing partial resorption of loop in front and greater divergence of descending branches. × 12.
10.—The same; profile. × 12.

Figure 11.—A little more advanced stage, showing increased length of connecting band. × 12. Specimens figures 7–11 are from the Trenton shales, *St. Paul, Minnesota.*

12.—A looped stage, with broad, curved, descending branches and more slender transverse band. × 6.

13.—The same; profile. × 6.

14.—A later stage, showing more slender loop. × 6.

15.—A specimen showing curved, diverging, descending branches, long transverse band, and two projections of the lamellæ, which are the beginning of the spiral cones. × 6.

16.—A subsequent stage in which the lamellæ are more extended and ventrally and inwardly curved. × 6.

17.—The same; profile. × 6.

18.—A young individual in which there are about one and one-half turns to each spiral. × 6.

19.—The same; profile. × 6.

20.—The brachial supports in a mature specimen. × 6. The specimens figures 12–20 are from the top of the Trenton, *Frankfort, Kentucky.*

21.—The spirals and loop in a Canadian specimen of (*Anazyga* =) *Zygospira recurvirostra.* (After Davidson.) × 3.

22.—The spirals and loop in (*Hallina* =) *Zygospira saffordi* W. and S. Trenton, *Tennessee.* × 6.

23.—The spirals and loop in (*Hallina* =) *Zygospira nicolletti* W. and S. Trenton, *Minnesota.* × 6.

24.—The spirals and loop in *Zygospira headi* Billings. (After Hall.) × 2.

25.—The spirals and loop in *Zygospira modesta* Say. (After Hall.) × $2\frac{1}{2}$.

26.—The same. (After Davidson.) × $3\frac{1}{2}$.